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Online-coupling of widely-ranged timescales to model coral reef development

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ABSTRACT

The increasing pressure on Earth's ecosystems due to climate change is becoming more and more evident and the impacts of climate change are especially visible on coral reefs. Understanding how climate change interacts with the physical environment of reefs to impact coral growth and reef development is critically important to predicting the persistence of reefs into the future. In this study, a biophysical model was developed including four environmental factors in a feedback loop with the coral's biology: (1) light; (2) hydrodynamics; (3) temperature; and (4) pH. The submodels are online coupled, i.e. regularly exchanging information and feedbacks while the model runs. This ensures computational efficiency despite the widely-ranged timescales. The composed biophysical model provides a significant step forward in understanding the processes that modulate the evolution of coral reefs, as it is the first construction of a model in which the hydrodynamics are included in the feedback loop.

1. Introduction

Coral reefs provide one of the most compelling examples of the impacts of increasing human pressures on the Earth's ecosystems (e.g. Hoegh-Guldberg et al., 2007; Hughes et al., 2019). Although local pressures such as overfishing and urban development can cause considerable impacts to adjacent coral reef systems, global pressures from climate change and ocean acidification are an overarching and ever increasing concern (Chan and Connolly, 2013; Bruno et al., 2019). For instance, mass bleaching events, which were extremely rare before the 1980s (Hoegh-Guldberg, 1999), have increased in frequency in recent decades and have become iconic examples of human-induced changes affecting life on the planet (Hughes et al., 2018).

Coral reef systems are highly valued for their role as biodiversity hotspots (Wilkinson, 2008), but are also critically important to the stability of other, associated, coastal ecosystems such as seagrass meadows and mangroves. Reefs are known to protect these systems from hydrodynamic (mostly wave) energy (Ferrario et al., 2014), while also exchanging food, nutrients and organisms with them (Gillis et al., 2014). Similarly, coral reefs also protect coastal communities against wave-driven flooding (Beck et al., 2018; Storlazzi et al., 2019) and coastal erosion (Sheppard et al., 2005). These ecosystem services are tightly coupled to the long-term development of reefs and their ecological state, thus understanding the processes controlling changes in reef condition is of critical importance (Denny and Gaylord, 2010; Helmuth et al., 2005; Kearney and Porter, 2009). The ability to predict the developmental capacity of corals depends on the proper modelling of the biophysical and ecological interactions between the reef and its environment (House et al., 2018).

In this paper, we present a proof-of-concept of a novel biophysical model that enables investigation of climate change related external forcing such as sea-level rise, temperature increases, and ocean acidification on coral reef development. The model concept is based on the interactions between key processes, categorized in three groups: (1) the direct physical environment of the coral; (2) the physiological state of the corals; and (3) the long-term morphological development (see Fig. 1). Modelling these feedback mechanisms provides a method of predicting the long-term development of coral-reef systems.

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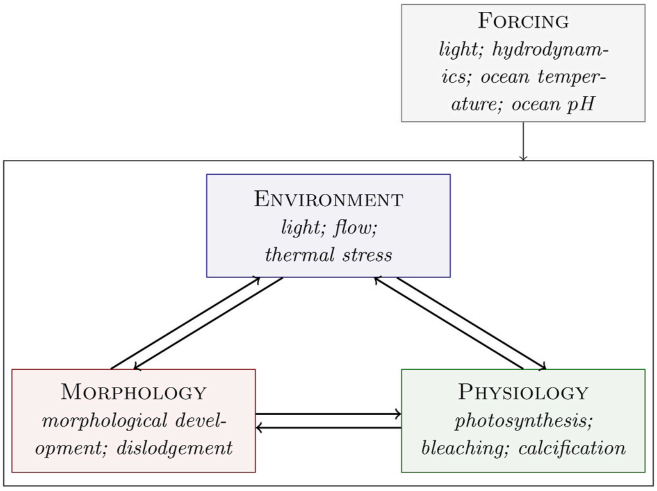

Fig. 1. Design of the biophysical model. The biophysical processes are described as two-way interactions between the environment (blue), coral physiology (green), and coral morphology (red), forced by long-term anthropogenic changes in the ocean (gray).

The effects of coral reef geomorphology on hydrodynamics—in particular on wave damping—has been extensively studied in recent years (e.g. Lowe et al., 2008; Weitzman et al., 2015; Zeller et al., 2015). The attenuation of the flow due to the (coral) canopy is an interplay between the characteristics of the canopy and the hydrodynamics. When the canopy is open, water can flow easily through the reef structure and so the damping is limited. This is a 'relative openness', as it is considered with respect to the wave conditions: the shorter the wave, the larger the open spaces inside the canopy are relatively. Long waves (e.g. tides) and currents are, therefore, attenuated more with the same canopy design compared to short waves (e.g. wind-waves) (e.g. Lowe et al., 2005a).

Compared to the timescale of hydrodynamics, coral-reef growth is an extremely slow process. Consequently, for the purpose of modelling hydrodynamics around reefs, reef geomorphology is considered constant in most applications (Hearn et al., 2001; Lowe et al., 2005b), or not taken into account at all (Buddemeier et al., 2008; Evenhuis et al., 2015; Silverman et al., 2007). However, for future projections at longer timescales—such as sea-level rise, temperature increase, or ocean acidification (i.e. order of decades)—consideration of coral growth and adjustments of coral morphology are important. Coral morphology is known to adjust directly to the environmental conditions (Todd, 2008) and depends on how physiological processes (photosynthesis, calcification) vary in relation to the environment (light, flow, temperature, pH) as a result: relationships that have been extensively described in the literature (e.g. Anthony and Hoegh-Guldberg, 2003; Donner, 2011; Evenhuis et al., 2015; Jimenez et al., 2011).

The aim of this study was to gain more insight into the key processes determining the development of a coral reef. This led to development of a biophysical model that is aimed to be robust, flexible, and process-based. The model describes the response of the coral-reef in terms of growth and survival to various environmental fluctuations. Flow and wave related information on the environment is derived from direct coupling to a hydrodynamic model. This coupling is two-way, as the feedback loop between the coral and its environment is closed by including the morphological development of the coral reef, and feeding that information back into the hydrodynamic computations; so-called online coupling.

Such coupled modelling poses challenges in model efficiency due to the wide-range of timescales involved, as the model time step is controlled by the smallest time scale. Therefore, methods to bridge the gaps between the timescales are explored in this paper. Holistic models that incorporate multiple timescales are important in understanding the future of coral reef development, as the processes playing at the various timescales are interconnected; e.g. wind-waves (order of seconds) affect the coral reef morphological development (order of millennia), which affects the wind-waves.

2. Model description

The core of the developed biophysical model is the feedback loop between the coral and its environment, where the coral's response is split in its physiology and its morphology (see Fig. 1). Part of the environment is considered as forcing and is not modulated by the coral reef (i.e. excluded from the feedback loop). The box "Environment" in Fig. 1 includes only the environmental factors that are included in the feedback loop. To model this feedback loop, requirements are: (1) adequate characterisation of the environment; (2) description of the physiological responses of the corals to the environment; (3) description of the morphological response of the coral to the environmental and physiological variations; and (4) feedback of the morphological adaptation to the hydrodynamic framework to translate it into renewed environmental parameters for coral growth and development.

The following environmental factors that are considered to influence the development of corals are included: (1) light; (2) water flow; (3) temperature; and (4) pH (Pratchett et al., 2015). Light is included due to the process of light-enhanced calcification, which describes the enhancement of the calcification rate due to photosynthesis of symbiotic zooxanthellae (Eyal et al., 2019; Goreau, 1959). The effects of flow are based on the supply and removal of nutrients and waste (e.g. Atkinson and Bilger, 1992; Hearn et al., 2001; Mass et al., 2010). The temperature is the primary cause of coral bleaching (e.g. Baird et al., 2009; Jokiel and Coles, 1977) as well as a general modifier of physiological and biochemical rates. Lastly, the pH is included by means of the aragonite saturation state, which can impact coral calcification rate and is the generally accepted approach to take into account ocean acidification in coral dynamics (e.g. Gattuso et al., 1998; Langdon and Atkinson, 2005; Ries et al., 2010).

The main processes in coral development are threefold: (1) growth; (2) degradation; and (3) recovery. In our model, degradation of coral reefs can result from two processes: bleaching-related mortality and storm damage (Hoegh-Guldberg, 1999; Madin and Connolly, 2006; Wilkinson and Souter, 2008). Other damaging processes—e.g. predation (Lenihan et al., 2015) and disease (Díaz and Madin, 2011)—were excluded as they cannot directly be related to the environmental factors included in this study. When the coral is damaged—and possibly dies—due to coral bleaching, its skeleton remains and influences the hydrodynamics; in case of storm damage, the coral is (partially) dislodged, which also affects the geomorphology of the coral-reef. These pathways are displayed in Fig. 2; bleaching events follow the right-hand side, and storm events the left-hand side.

2.1. Coral environment

The morphology of corals affects both the macro- and micro-environments that surround them (e.g. Jimenez et al., 2011; Lowe et al., 2005a; Monismith, 2007). Due to this feedback, the environmental conditions environing the coral may differ from the ambient water. Therefore, the micro-environments related to light, flow, and temperature are discussed below. The micro-environment related to pH was left out because it was considered homogeneous over a coral reef due to (1) the small depth over a coral reef; and (2) the well-mixed water column due to turbulence (e.g. Reidenbach et al., 2006b).

2.1.1. Light micro-environment

Light attenuates with depth (Freitas et al., 2019; Kratzer et al., 2003), where the light that can be used for photosynthesis depends on the coral's morphology due to shading effects (Hoogenboom et al., 2008; Muko et al., 2000; Stambler and Dubinsky, 2005). Therefore, a

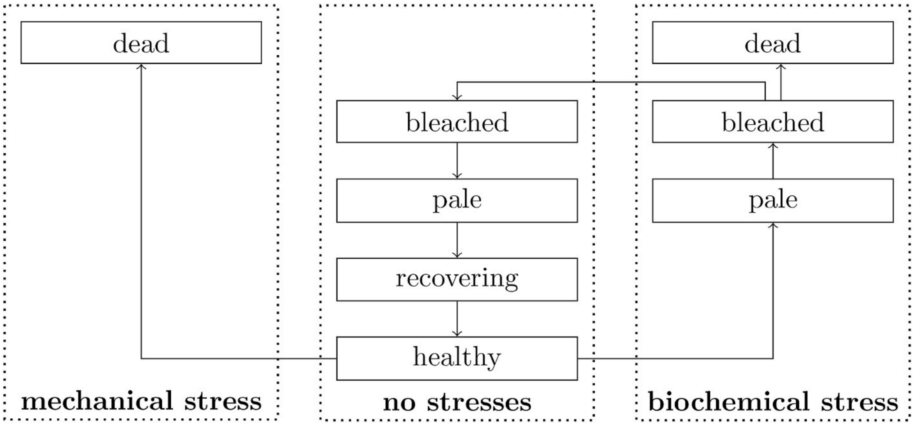

Fig. 2. Pathways of loss and damage of corals due to environmental stresses. The mechanical stresses indicate the pathway due to coral dislodgement, i.e. due to storm events; the biochemical stresses indicate the pathway due to coral bleaching, i.e. due to bleaching events. The population states are further specified in Section 2.4.1 (modified from Evenhuis et al., 2015).

representative light-intensity was determined based on the light micro-environment. This representative light-intensity was defined as the biomass-averaged light-intensity. Here, the biomass was defined as the surface of the coral receiving light (green shading in Fig. 3; Allemand et al., 2004; Jokiel, 2011; Hoegh-Guldberg, 1988). The definition of the biomass incorporates the spreading of light to determine the extent of the shading (see Fig. 3), where this spreading reduces with increasing depth (Jokiel, 2011).

2.1.2. *Flow micro-environment*

The presence of corals—collectively a coral canopy—highly influences the hydrodynamics: both waves (e.g. Lowe et al., 2009; Monismith et al., 2015) and currents (e.g. Baptist, 2005; Nepf and Vivoni, 2000; Nikora et al., 2013). Only an attenuated flow remains within the coral canopy (e.g. Lowe et al., 2005a; Weitzman et al., 2015; Zeller et al., 2015), here termed the flow micro-environment. This flow micro-environment is important for the supply of nutrients and the removal of waste (Lowe et al., 2005b; Reidenbach et al., 2006a). For the characterisation of the flow micro-environment we used the wave attenuation formulations of Lowe et al. (2005a) and Zeller et al. (2015). The flow attenuation in the canopy was modelled following Zeller et al. (2015) and van Rooijen et al. (2018). Wave- and current-induced flows were assumed to interact linearly (Bijker, 1967; Lowe et al., 2005a). The drag coefficient was determined dynamically (Etminan et al., 2017; van Rooijen et al., 2018).

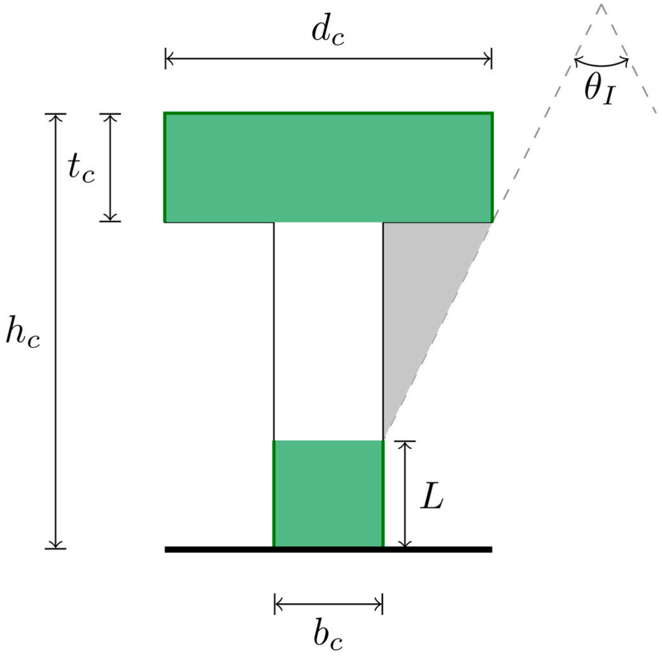

Fig. 3. Schematisation of a coral morphology including the definition of the biomass. d_c is the width of the plate; h_c the coral height; b_c the width of the base; t_c the thickness of the plate; θ_I the spreading of light; and L the section of the base that receives light. The area contributing to the photosynthesis—i.e. the biomass—is accentuated with green; and the gray-shaded area represents the shading due to the morphology.

2.1.3. *Thermal micro-environment*

The thermal micro-environment may result in an increased temperature up to 1 °C above the ambient water (Brodersen et al., 2014; Fabricius, 2006; Jimenez et al., 2011). This discrepancy arises due to the presence of a thermal boundary layer, which is related to the flow micro-environment through the turbulent boundary layer (Jimenez et al., 2011). Within this boundary layer, diffusive transport dominates over advective processes; in addition the illuminated surface of the coral acts as a source of heat, leading to a local temperature elevation. The temperature within the thermal boundary layer is the actual temperature experienced by the coral and is potentially important in determining critical boundaries for the occurrence of thermally-induced bleaching (see Secs. 2.2.3 and 2.4.1). For the definition of the thermal micro-environment, we followed the formulations by Jimenez et al. (2011).

2.2. *Coral physiology*

Coral physiology describes the rate of growth of individual corals, which is described using the calcification rate. The calcification rate was defined as the product of environmental dependencies and two calibration parameters (based on Evenhuis et al., 2015). Whereas this forms a linear basis, non-linearities can be included due to the formulations of the environmental dependencies of growth. An important factor modulating calcification rate is the photosynthetic dependencies due to the principle of light-enhanced calcification (Eyal et al., 2019; Goreau, 1959). These photosynthetic dependencies include the effects of light, temperature, and flow; where the pH only affects the calcification rate. This section describes all four environmental dependencies included.

2.2.1. *Photosynthetic light dependency*

The photosynthetic light dependency is given by the photosynthesis-irradiance curve (e.g. Chalker et al., 1983; Jassby and Platt, 1976). To reduce the number of input parameters, the dark respiration was defined such that the net photosynthesis equals zero at the base of the euphotic depth zone, defined as the depth with 1% light penetration. The remaining parameters—maximum photosynthetic rate and saturation light-intensity—were dynamically modelled, depending on photo-acclimatisation. Formulations on the photo-acclimatisation follow Anthony and Hoegh-Guldberg (2003) and Chalker et al. (1983).

2.2.2. Photosynthetic flow dependency

Photosynthesis depends on flow through the diffusive boundary layer, where transport is diffusion-limited (Atkinson and Bilger, 1992; Hearn et al., 2001; Mass et al., 2010). The presence of a diffusive boundary layer can limit the supply of nutrients, as diffusion is much slower than advection (e.g. Jimenez et al., 2011). Within the diffusive boundary layer, the transport rate is described by Fick's first law, where the concentration gradient was assumed linear and consequently the transport rate is inversely related to the thickness of the diffusive boundary layer (Jimenez et al., 2011; Mass et al., 2010). The thickness of the diffusive boundary layer is inversely related to the flow velocity (e.g. Absi, 2009), resulting in a linear relationship between the photosynthetic flow dependency and the flow velocity (in line with Comeau et al., 2014; Lenihan et al., 2015). However, photosynthesis is not flow-limited for velocities above 0.10 ms^{-1} (Hurd, 2000), the linear relationship was capped at this point using a tangent-hyperbolic function to avoid discontinuities.

2.2.3. Photosynthetic thermal dependency

Photosynthetic thermal dependency describes the thermal limitations on the symbiosis between the coral animal and its zooxanthellae, together known as the coral holobiont (Baird et al., 2009). Two components were distinguished: (1) the adapted temperature response; and (2) the thermal envelope (Evenhuis et al., 2015).

The adapted temperature response describes the thermal range in which the symbiosis functions normally. Between a lower and a higher temperature, a cubic equation with an optimum in between the limits describes the dependence of the symbiosis on temperature. Thermally specialised coral species have narrow ranges and high optimal rates; eurytopic coral species have broader ranges but lower optimum values. The thermal envelope expresses the principle of increased biochemical reactions at higher temperature—according to the Arrhenius equation (Evenhuis et al., 2015). In between the thermal limits, all rates are higher as the limits shift to higher temperature ranges.

The limits of the thermal range are not fixed but (slowly) adapt to the temperatures the coral holobiont has experienced over time (Donner, 2011; Logan et al., 2014; Palumbi et al., 2014). The formulation for this thermal-acclimatisation was based on, but modified from, the principle of degree heating weeks (following Donner, 2011): the upper and lower limits of the thermal range were based on a running mean of the respectively monthly maximum and minimum means over a period of 60 years, when possible (this period is based on Logan et al., 2014).

2.2.4. Ocean pH dependency

The oceanic carbon system consists of a complex interplay between the different forms of dissolved inorganic carbon and pH (Mucci, 1983; Roy et al., 1993; Weiss, 1974). In the model, this complexity has been reduced to a dependency of calcification on the aragonite saturation state, as is common practice in coral studies (Gattuso et al., 1998; Langdon and Atkinson, 2005; Ries et al., 2010). The dependency was modelled as a modification of the Monod equation.

2.3. Coral morphology

A schematic of the coral's morphology (Figs. 3 and 4) is included in the model to estimate the rates of several processes. Light reaching the surface of the coral is an example of such a process. Other examples are flow and wave attenuation, and dislodgement of corals by storms.

To keep the formulations manageable but still retain the possibility to represent the major types of corals, the coral morphology was simplified to a tabular shape, i.e. a two-layer cylinder. In literature, the coral is often represented by simpler cylindrical shapes (e.g. Lowe et al., 2005a; Storlazzi et al., 2005; Zeller et al., 2015). Here, a two-layer cylinder is used to better represent storm damage (see Sec. 2.4.2). Furthermore, a two-layer cylinder does not exclude the representation of cylindrical shapes—such as massive coral colonies—but it increases the possibility of representing coral morphologies (see Fig. 4 for a range of morphologies).

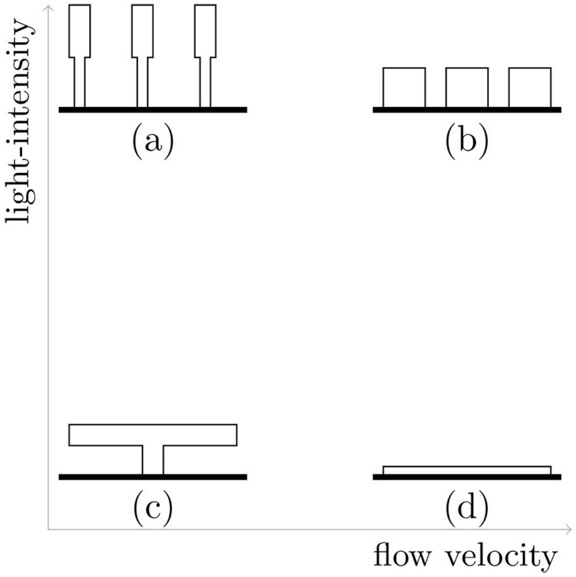

Fig. 4. Schematic representation of the influence of the environment on the coral morphology. Coral morphologies are simplified to cylindrical shapes, as used in this study. **(a)** branching; **(b)** fingered, columnar; **(c)** tabular; **(d)** massive, encrusting.

Coral morphology is a trait with high phenotypic plasticity (i.e. the morphology of a particular species can vary based on local environmental conditions; Todd, 2008). The optimal morphology of a coral in a location is based on a multitude of environmental factors (Chappell, 1980) of which only the light and flow conditions were included in this study.

To determine the optimal morphology, qualitative descriptions from literature were used as a basis for quantitative relationships in the model. High light-intensity results generally in vertically-directed growth, whereas low light-intensity promotes horizontal growth (e.g. Chappell, 1980; Hoogenboom et al., 2008; Muko et al., 2000). High flow velocity enhances the compactness of the coral's morphology, whereas low flow velocity results in more fragile structures (e.g. Kaandorp, 1995; Kaandorp and Sloot, 2001; Kruszyński et al., 2007). A schematic overview of the optimal morphology due to environmental gradients is presented in Fig. 4.

The morphological development was described by a set of partial differential equations, directing the morphological parameters in the direction of optimal morphology for the governing conditions. Morphological adaptations were constrained by the mass balance, as the calcification rate sets the boundaries for the possible rate of change of the morphology.

2.4. Coral survival

The coral survival was related to three key processes: (1) coral bleaching; (2) coral dislodgement; and (3) coral recruitment. Although these processes occur at different timescales, they are grouped in this section due to their overlapping topic.

2.4.1. *Coral bleaching*

When a coral bleaches, it passes multiple states before it dies (Baird and Marshall, 2002; Lough et al., 1999). In this study, we included four such states after Evenhuis et al. (2015): (1) healthy; (2) pale; (3) bleached; and (4) recovering (see Fig. 2). This is in line with other studies, except the addition of the recovering state (Jokiel and Coles, 1977; Marshall and Baird, 2000). In this state, the coral seems healthy (i.e. it has recovered its pigmentation) but it has not yet resumed growth (Evenhuis et al., 2015).

The total population cover at space x and time t was described by a vector composed of the cover of each of the four population states. The dynamics of this population were described by a set of partial differential equations expressing the transitions between the different states (following Evenhuis et al., 2015). These dynamics were related to the photosynthetic efficiency, as this expresses the most direct response to the environmental conditions, as discussed earlier. Calcification rate was constrained by photosynthetic rate as its main source of energy, but in addition also depends on the population states as only healthy corals are capable of growth.

2.4.2. *Coral dislodgement*

The leading mechanism for dislodgement of coral colonies is a storm event because the substratum is in general substantially weaker than the coral skeleton itself (Macintyre and Marshall, 1988; Madin, 2005; Madin et al., 2013). This damage can be direct, due to the wave load directly impacting on the coral structure (Madin, 2005; Madin and Connolly, 2006; Storlazzi et al., 2005). It can also be indirect, due to tumbling coral fragments (Knowlton et al., 1981; Smith and Hughes, 1999). The direct damage can further be categorized in breakage of the coral skeleton (Chamberlain, 1978; Schuhmacher and Plewka, 1981) and dislodgement of the whole coral colony (Hongo et al., 2012; Madin, 2005; Madin and Connolly, 2006).

We used the dislodgement model of Madin and Connolly (2006), due to its simplicity but still proven robustness (Hongo et al., 2012). This model defines a dislodgement criterion consisting of two dimensionless parameters: (1) dislodgement mechanical threshold (DMT); and (2) colony shape factor (CSF). The first relates the strength to the load, and the latter includes the effect of the morphology.

This model has a binary nature: dislodgement happens or not. In combination with the simplifying assumption that only a single morphology occurs per computational cell, it results in the undesirable feature that either all corals from a cell disappear, or all stay in place. To avoid this binary response, the model of Madin and Connolly (2006) was modified to represent a continuous relationship between the load (i.e. dislodgement mechanical threshold) and the resistance (i.e. colony shape factor).

2.4.3. *Coral recruitment*

Bleaching and storm events may cause the complete disappearance of living coral cover on a reef section. However, this does not necessarily mean that this reef section will never be repopulated. To include this recovery mechanism, the recruitment of corals has to be taken into account. Coral recruitment was simplified to an annual contribution to the coral cover and volume, representing a mass spawning event of corals (Guest et al., 2005; Mangubhai and Harrison, 2008; Vize, 2006).

3. Timescales

The processes that control coral-reef development span a wide range of timescales, as presented in Fig. 5. Waves vary over the order of seconds (e.g. Holthuijsen, 2007), while the morphological development of a reef occurs over the order of decades to millennia (e.g. Lough et al., 2016; Toth et al., 2018).

Updating the morphological development every second would not yield significant differences in the morphology. Conversely, modelling wave conditions over scales of decades and beyond would be computationally prohibitive. Therefore, the processes were split into modules and coupled at different intervals; a method commonly used in hydrodynamics and morphodynamics. This online-coupling principle is illustrated in Fig. 6.

The smallest basic time-interval is used by the hydrodynamic model, which updates at a timescale of seconds. The upper limit of this time step is determined by the stability criteria that govern hydrodynamic models. Physiological rates of the corals were updated with a time step of days, implying that day-averaged conditions for light, thermal, hydrodynamic, and acidic conditions were used to drive the physiology. Morphological adjustments used an annual time step. In this way, unnecessary long calculations were avoided, as not all adjustments have to be performed at the stability-limited time step of the hydrodynamic model.

To further accelerate the model, two acceleration methods from the fields of hydrodynamics and morphodynamics were considered: (1) input reduction; and (2) model reduction (Li et al., 2018).

The method of input reduction focuses on reducing the hydrodynamic input parameters by determining a representative set of wave conditions based on the full wave climate (Benedet et al., 2016; Walstra et al., 2013). In this study, this method was implemented to its extreme by defining one set of wave conditions representing ‘normal’ conditions for one year. In addition, storm conditions were defined, which hit the reef based on their return periods. When—based on randomness—a storm ‘occurred’, the hydrodynamic model was used to simulate the storm hydrodynamics. This may lead to (partial) damage to the reef, which was updated accordingly (see Sec. 2.4.2).

The method of model reduction aims at reducing the number of input parameters and model processes (Li et al., 2018). In the balance between a computationally efficient but less complete model, versus a complete but expensive model, this approach attempts to exclude the formulations that bring the least information compared to their cost. Here, we evaluated costs and benefits for the three computationally most expensive processes: (1) calculating the thermal micro-environment; (2) calculating the flow micro-environment; and (3) including the flow in the physiology all together (but retaining the coupling with the hydrodynamic model for simulating storms).

4. Model coupling

To create the feedback loop between the biological and physical processes, the biological model was coupled online to the Delft3D Flexible Mesh hydrodynamic model (Deltares, 2019), in which short waves were simulated using the SWAN wave model (Booij et al., 1999). Delft3D Flexible Mesh is a process-based numerical model that solves the Navier-Stokes equations. For the purposes in this study, the hydrodynamics were determined based on depth-averaged 2D simulations. This study has not modified the hydrodynamic model in any way, only an online coupling with the biological component has been established.

The newly developed coral-reef model, as described in this paper, was written in Python. The model code controlled both the biological and the hydrodynamic modules, using the BMI-wrapper[1] for this online coupling. The Python code initialised the hydrodynamic model, called the hydrodynamic calculations for the duration of one biological step, updated the coral physiology and growth, stored the contribution to morphological development, then started a new coral growth time step. After simulation of the coral growth for one year, the morphology was updated and the changed morphology was fed into the hydrodynamic model, after which a new series of coral growth steps was performed. This so-called online coupling of the different model components is one of the novel aspects of the developed biophysical model.

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[1] The BMI-wrapper is a package in Python that enables the control of Delft3D Flexible Mesh from Python. This package can be downloaded from GitHub: https://github.com/openearth/bmi-python.

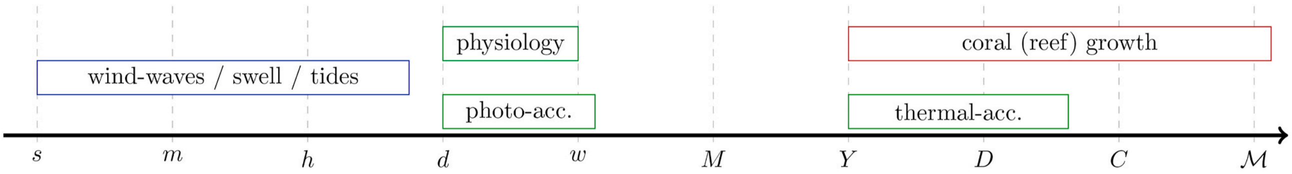

Fig. 5. Timescales of the processes included in the developed biophysical model. acc.: acclimatisation; *s*: seconds; *m*: minutes; *h*: hours; *d*: days; *w*: weeks; *M*: months; *Y*: years; *D*: decades; and *C*: centuries; 𝓜: millennia.

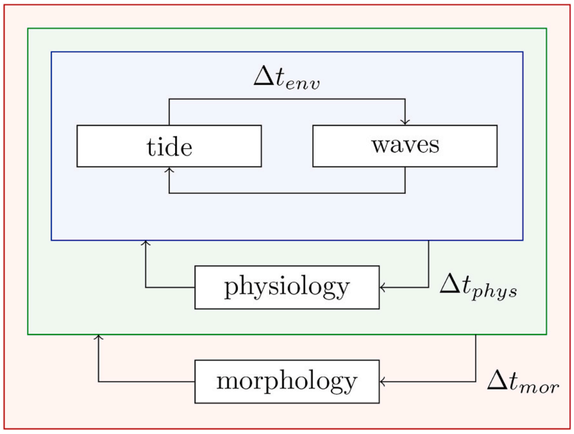

Fig. 6. Schematisation of the coupling between different parts of the coral growth model. Both the tide and the waves (includes wind-waves and swell) are computed using the hydrodynamic model, which couples these models online with a frequency as given by Δt_{env}; Δt_{phys} is the time-interval between every online coupling between the hydrodynamic model and the physiological processes; and Δt_{mor} is the time-interval at which the morphology is coupled to the rest of the model.

5. Model validation settings

5.1. Process validation runs

The validation of the biophysical model was performed per process, as no data set was available that covered all aspects. Furthermore, Bellocchi et al. (2009) suggests the use of modular validation runs for complex models as the one developed in this study. These runs were based on single or grouped field studies, as indicated below. In the validation runs, the environmental conditions as described in the studies were replicated and the model results were compared with the published data. Not all validation runs are presented in this paper for readability.

5.1.1. Calcification rate

Calcification rate was considered as one of the key processes to validate the biophysical model to, as it determines the growth rate of the corals and the coral reef as a whole. For this validation, field data from multiple studies were used that covered multiple sites per study (Howells et al., 2018; Lough and Barnes, 2000; Lough et al., 2016; Scoffin et al., 1992). These long-term calcification rates were compared to the model results. In all studies, the reefs were considered spatially homogeneous; no spatial variations of calcification rate within the reef could be studied. Therefore, the validation of the calcification rate is based on reef-scale averages, which putatively includes many species. The field data and the model results were compared by means of the root-mean-squared error.

5.1.2. Bleaching

The modelling of bleaching processes was validated using bleaching reports and studies describing the response of multiple coral species to thermal stresses in a diversity of studies: Baird and Marshall (2002); Bayraktarov et al. (2013); Berkelmans and Van Oppen (2006); Dias et al. (2018); Howells et al. (2013); Jokiel and Coles (1977). From this list of validations, we highlight one of these studies in which multiple aspects are incorporated, namely the study by Howells et al. (2013). In this study, corals were transplanted between the central and the southern regions of the Great Barrier Reef to investigate the importance of thermal acclimatisation. With this approach, Howells et al. (2013) not only report on the onset and aftermath of bleaching, but also on the determination of the thermal limits. Even though Magnetic Island—which is part of the study by Howells et al. (2013)—is a marginal reef, the study provided excellent validation material because it includes multiple facets of the developed model, and so functions as a good illustration for this proof-of-concept study.

5.2. Integrated model runs

To test and examine the coupled model, an archetypical fringing reef was defined on which representative environmental conditions were applied. This fringing reef starts at the sea surface and reaches a depth beyond the euphotic depth. Light input, temperature, wave impact and currents were loosely based on conditions on the Great Barrier Reef[2] and extrapolated to simulate a hundred years with a realistic frequency of storms of different severity.

The spatial domain of the model used for these integrated model runs was 200 m in alongshore direction, and 600 m in cross-shore direction; and a spatial resolution of 2.5 × 2.5 m was used. This spatial domain and resolution was used for the whole biophysical model; i.e. also for the biological component. The spatial domain of the coupled waves-module—i.e. SWAN—is much wider to limit the influence of the boundaries in the region of interest; due to wave spreading, the waves flatten at the boundaries of the model domain. The spatial domain of this enlarged spatial domain was 1000 m in alongshore direction, and 700 m in cross-shore direction; and a spatial resolution of 10 × 10 m was used.

The validation of storm damage on the coral reef was only qualitative, due to lack of quantitative data on the subject. Most emphasis was placed on the evaluation of the depth gradient in storm damage.

For the evaluation of the input reduction strategy, the hydrodynamics were updated once per year due to the slow growth of corals that impose little changes on the timescale of years. This strategy assumes that daily fluctuations in wave conditions have little effect on the coral development. The influence of this assumption was evaluated by considering the effects of a difference in wave height up to approximately 20% on both the calcification rate and the bleaching response.

Several runs were performed to test strategies for model reduction. In the evaluation of the model reduction, the sensitivity of the model output to the exclusion of selected processes (related to thermal and flow boundary layers, and to any flow interaction with physiology, see Sec. 3) was assessed in combination with the resulting reduction in simulation

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[2] Light conditions were based on the orbit of the Earth and the latitude; the hydrodynamic conditions were based on literature (Madin, 2004, 2005; Massel and Done, 1993); thermal conditions were based on sea surface temperature from NOAA OI SST V2 High Resolution Dataset provided by the NOAA/OAR/ESRL PSD, Boulder, Colorado, USA, from their Web site at https://www.esrl.noaa.gov/psd/.

time.

6. Results

6.1. Process validation runs

Due to the biophysical model's complexity, first a modular validation was performed as suggested by Bellocchi et al. (2009), which showed good agreement. Here, only the validation of the biophysical modelling of coral cover and calcification rate are presented in Figs. 7 and 8, respectively. These validations are discussed in more detail below.

In the study of Howells et al. (2013)—introduced in Section 5.1.2—corals were transplanted from two different locations on the Great Barrier Reef hundreds of kilometres apart: Magnetic Island is located in Central Great Barrier Reef; and Miall Island is located in Southern Great Barrier Reef. Due to their different temperature histories, their thermal limits differ and so their responses to the thermal conditions. During the study period, a bleaching event occurred at Magnetic Island due to heat stress (see Fig. 7, left column); and a bleaching event occurred at Miall Island due to cold stress (see Fig. 7, right column). As the corals from Miall Island were acclimated to colder temperatures, the damage due to the bleaching event at Magnetic Island was substantially more severe. The cold-water bleaching event at Miall Island resulted in almost no bleaching for the corals from Miall Island—which were more adapted to colder temperatures—while severe bleaching occurred among the corals originating from Magnetic Island. Unfortunately, the Central Great Barrier Reef was affected by flooding during the study period (see Fig. 7), resulting in significant additional coral mortality (Howells et al., 2013). The data from Howells et al. (2013) after this flooding event were not taken into account in the assessment of the model validation. Overall, the model simulated the effects of a bleaching event and its aftermath reasonably well. However, it did not completely follow the field data. Almost certainly, a better match could have been achieved with parameter tuning, but that was not the aim of this study.

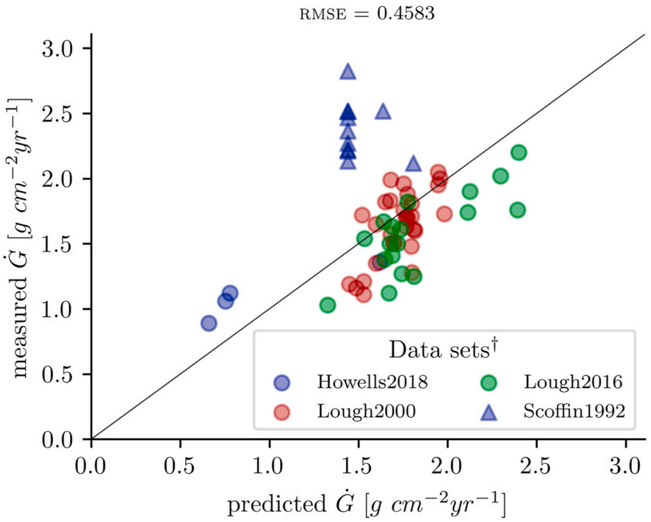


Fig. 8. Validation of the modelled calcification rate with field measurements presented in the literature. The root-mean-squared error (RMSE) is presented on top. † Sources: Howells2018, Howells et al. (2018); Lough2000, Lough and Barnes (2000); Lough2016, Lough et al. (2016); Scoffin1992, Scoffin et al. (1992).

In the validation of the calcification rate, one parameter remained open to be fitted to the data: the calcification constant. The four studies considered (Howells et al., 2018; Lough and Barnes, 2000; Lough et al., 2016; Scoffin et al., 1992) spanned a wide spectrum of different

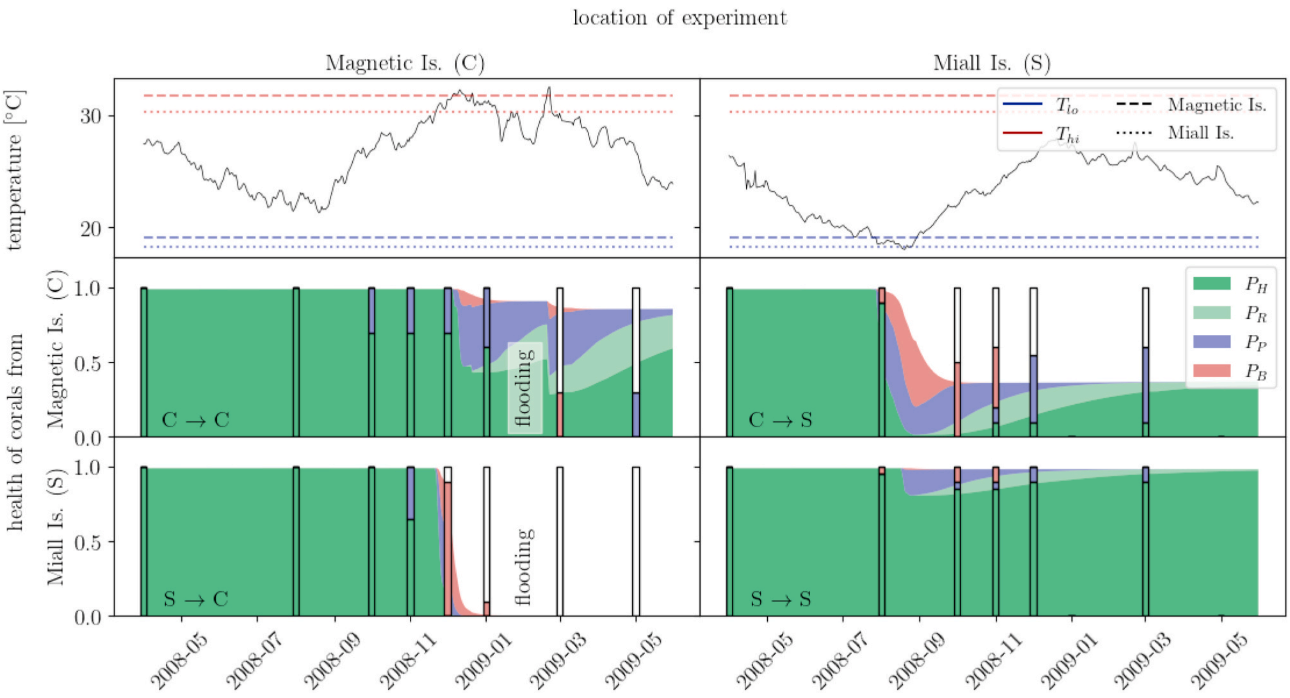


Fig. 7. Validation of coral health data highlighting the difference between temperature history. Corals from two different locations at the Great Barrier Reef (GBR) were transplanted to illustrate the relevance of the temperature history on the response on thermal conditions, where Magnetic Island is located in Central GBR; and Miall Island in South GBR. Top panels present the in-situ measured sea-surface temperature data, including the lower and upper thermal limits (T_{lo} and T_{hi}, resp.) based on the coral's origin. Other panels represent the response of the corals as the population dynamics; middle panel shows corals originating from Magnetic Island, and bottom panel originating from Miall Island. Bars indicate the measurements conducted during the experiments, and the continuous areas represent the model output; both follow the same color scheme: P_H is healthy coral cover; P_R recovering coral cover; P_P pale coral cover; and P_B bleached coral cover. More details are presented in the text (data from Howells et al., 2013).

environmental conditions, locations, and coral species. From these studies, a best estimate for the calcification constant was $g_C = 0.5$ kg m^{-2}d^{-1}. A substantial fraction of the within-study and cross-study variation in calcification rates was covered by the model (see Fig. 8), and little systematic bias was present in the model predictions. Part of the variation in the observed data, however, remains unexplained. Although, there is a known difference in calcification rates between Indo-Pacific reefs and western Atlantic reefs (Dullo, 2005), which may require re-tuning of this parameter depending on the location of interest.

The model performance on storm damage was only evaluated qualitatively due to a lack of data on storm impacts. The representative reef, used for the test of the integrated model, was also used to establish the reaction to storm disturbance. The results clearly illustrate the effects of depth on the dislodgement (Fig. 9). Beneath a threshold depth of approximately five metres there was no storm damage. Damage increased with decreasing water depth.

6.2. Model acceleration

The validity of the imposed input reduction was assessed by means of a sensitivity analysis during ‘normal’ wave conditions. The results indicate that a change in approximately 20% of significant wave height did not impose substantial differences in coral development as defined by coral cover (Fig. 10a) and coral volume (Fig. 10b).

The effects of the model reductions were also assessed by means of a sensitivity analysis in which the coral development of an ideal fringing reef were simulated for hundred years. The duration of the simulations is presented in Table 1,[3] where the relative difference is of importance: the biophysical model is 40 times faster—and so computationally less expensive—when the biological part is only coupled with the hydrodynamic model to simulate storm events. The outcomes of the configurations were within the accuracy of the input parameters for long-term simulations (see Fig. 11), in this case derived from climate projections.

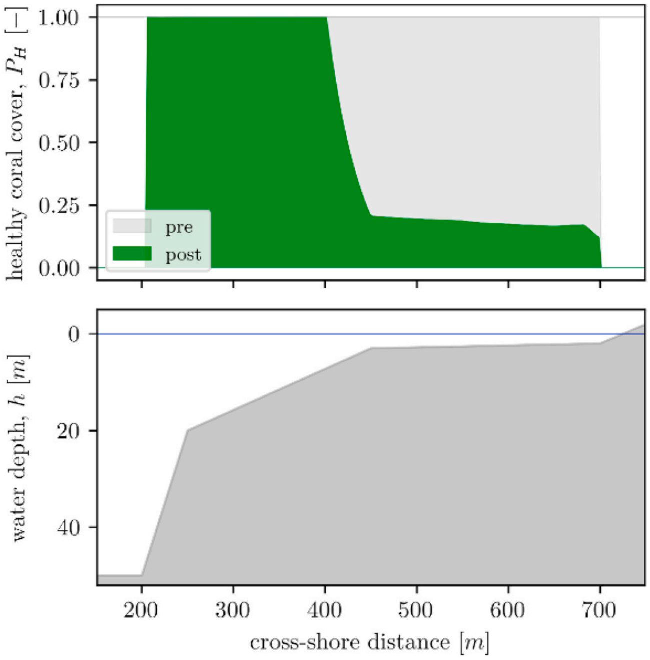
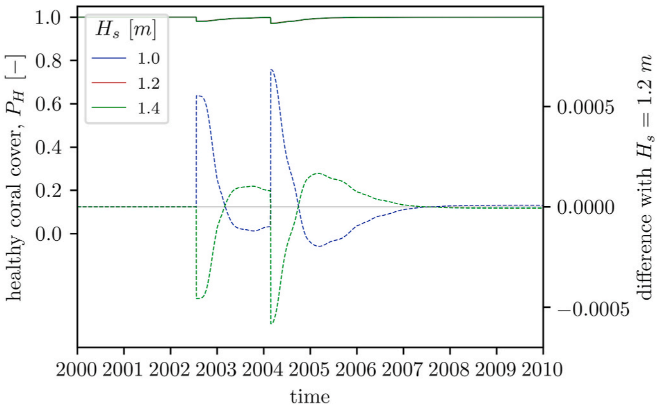
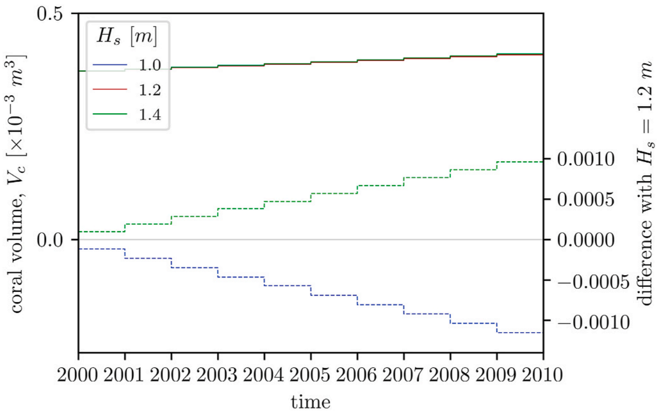


Fig. 9. Spatially varying dislodgement response due to a storm event. The upper panel presents the spatially varying damage of a coral reef—*pre* and *post* storm—by means of the healthy coral cover, P_H. The bottom panel shows the corresponding bathymetry of the reef with the blue line representing mean sea level.



(a) Healthy coral cover.



(b) Coral volume.

Fig. 10. Sensitivity of the coral development to the wave climate of the ‘normal’ conditions. The effects of the significant wave height (H_s) as used under ‘normal’ conditions on **(a)** healthy coral cover; and **(b)** coral volume. Note the different orders of magnitude between the absolute values (left axis) and differences (right axis). The red lines ($H_s = 1.2$ m) in both panels merge with the other settings in the absolute sense (left axis), and the differences are relative to this significant wave height and so by definition zero (right axis).

Table 1
Simulation time per configuration considered in the model reduction. Configuration 0 includes all process and can be considered the ‘base case’; Configuration 1 includes all except the thermal micro-environment (TME); Configuration 2 includes all except the thermal and flow micro-environments (TME and FME); and Configuration 3 only couples the biological part with the hydrodynamic model to simulate storm events, and so excludes also the photosynthetic flow dependency (PFD).

Configuration		Time [hours]
0	PFD + FME + TME	40
1	PFD + FME	12
2	PFD	8
3		1

7. Discussion

This proof-of-concept study shows that the developed biophysical model enables the simulation of long term coral reef development against low computational costs. The results of this conceptual study show that the main determinants of long term coral reef development

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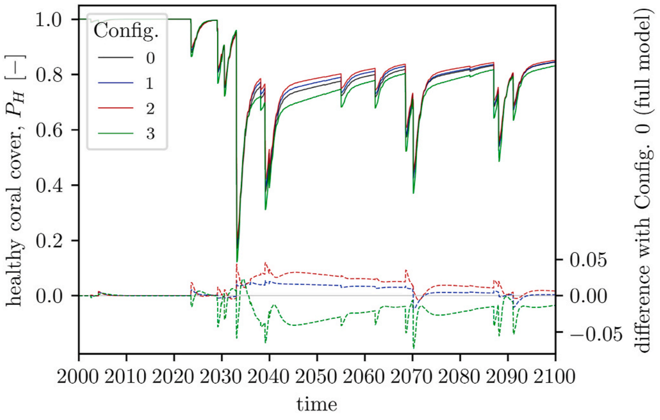
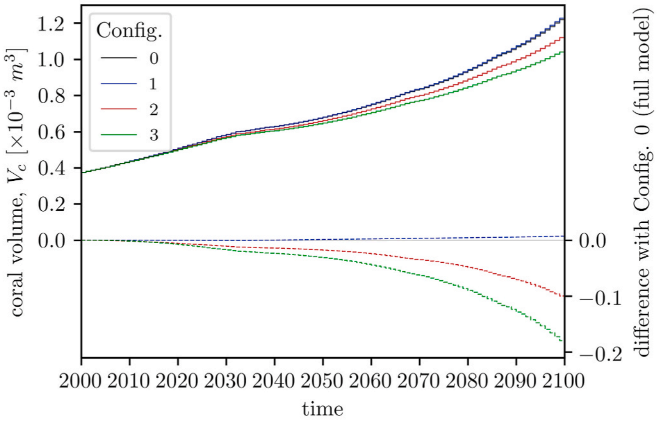
[3] Simulations were executed on a server with 4 cores, 3.5 GHz, 16 GB RAM.



(a) Healthy coral cover.



(b) Coral volume.

Fig. 11. Sensitivity of the coral development to the thermal micro-environment. See Table 1 for the labelling of the configurations. The most extreme effects are presented for **(a)** the coral cover, which is located in deep water; and **(b)** the coral volume, which is located in shallow water.

are the occurrence and severity of bleaching and storm events; and the capability of the reef to recover from such events. Furthermore, the developed biophysical model is—as was aimed for—robust, flexible, and process-based.

7.1. Model design

The biophysical model developed in this study was based on previous models representing physiological processes (Buddemeier et al., 2008; Evenhuis et al., 2015; Silverman et al., 2007) as well as storm damage (Madin, 2005; Madin and Connolly, 2006). What is different about our new setup is the connection between these different processes, and between the biological and physical aspects of coral development, which previously were separated. Because the size and morphology of corals are key in their dislodgement susceptibility (Madin and Connolly, 2006; Storlazzi et al., 2005), the growth rate and shape are important characteristics to incorporate when making long-term predictions. On the other hand, the coral's size and shape are highly influenced by the hydrodynamics, and the other environmental factors. Evenhuis et al. (2015) developed a physiological model—which is at the basis of the physiological processes in this study—that is able to predict the physiology well, but they did not take storm damage into account. On the other hand, Madin and Connolly (2006) and Storlazzi et al. (2005) developed models to simulate storm damage when the coral morphology is considered known, which makes them unsuitable for long-term predictions as the reef morphology develops over time.

The core of the developed biophysical model is linear, where the effects of the environmental factors on the growth rate of the coral are expressed by means of dependencies; e.g. the photosynthetic light dependency is multiplied by the photosynthetic thermal dependency. This allows for the addition of other dependencies not yet incorporated, such as nutrients.

This linear structure of the core does not exclude the incorporation of non-linear cross-dependencies, such as the combined effects of light, flow, and thermal conditions that are encapsulated in the thermal micro-environment. Other non-linear cross-dependencies can be added in a similar fashion.

Furthermore, the biophysical model is an efficient tool to make predictions of coral reef development, as different levels of detail can be achieved (see Table 1).

The biophysical model contains two parameters that can be used to accommodate for the physiological differences between coral species: (1) the species constant; and (2) the calcification constant. The species constant reflects the different survival tactics of a coral species, where slow growers are commonly less susceptible to bleaching than fast growers (Evenhuis et al., 2015; Marshall and Baird, 2000). This species constant is part of the formulations of the calcification rate and the bleaching response. The calcification constant allows for further tuning of the coral calcification rate to available data. The results of this study show that the order of magnitude of this calcification constant is $g_C = 0.5$ kgm^{-2}d^{-1}. The current model design does not allow for multiple values of the two parameters per simulation. Thus, these parameters are to be tuned to reflect the coral reef as it is populated by one type of coral species. The option to simulate different coral species per simulation is the goal of further developments of the biophysical model. This addition is most likely to add to the accuracy of the model results and would enable the option to simulate the dynamics of a coral reef ecosystem.

In addition, the morphological development of the coral can be tuned by means of a set of parameters describing the sensitivity of the coral morphological development to the environmental factors. Here, the volumetric expansion of the corals is linearly related to the calcification rate, as there is a strong correlation between calcification rate and linear extension (e.g. Lough, 2008; Pratchett et al., 2015) suggesting a similar correlation between calcification rate and volumetric expansion.

7.2. Model efficiency

The input reduction has been used to its extreme because this study is a proof-of-concept of the biophysical model. Nevertheless, the results suggest that this level of reduction is more generally applicable due to the limited differences in the physiological response on the wave conditions (see Fig. 10).

The limited effect of excluding the thermal micro-environment as part of the model reduction on the outcomes is in line with the fact that coral health and reef development is often related to the sea-surface temperature instead of the thermal micro-environment (Buddemeier et al., 2008; Donner, 2011; Evenhuis et al., 2015; Silverman et al., 2007). The differences that arise from excluding the flow micro-environment are limited because the flow is only used for the photosynthetic flow dependency, which is evenly well-fitted to the in-canopy flow as to the bulk flow. Because the photosynthetic flow dependency is commonly a secondary research topic (Atkinson and Bilger, 1992; Mass et al., 2010; Schutter et al., 2011)—and there is still large uncertainty with it—excluding this process results in flow independence of the physiology, which is often modelled as such (Buddemeier et al., 2008; Silverman et al., 2007; Evenhuis et al., 2015).

The results from the input and model reduction comply with each other, as they both indicate the irrelevance of the flow conditions on the physiology of corals under 'everyday' conditions. However, completely decoupling the biological processes from the hydrodynamics excludes the effects of storms. This would hamper the modelling, as storm events have a significant influence on coral reefs (Scheffers and Scheffers, 2006; Wilkinson and Souter, 2008).

Furthermore, other processes that are not yet included in the biophysical model rely on more detailed hydrodynamic information such as sedimentation (Luijendijk et al., 2019; Ranasinghe et al., 2011), and larval dispersal (Bradbury and Snelgrove, 2001; Cowen et al., 2006; Cowen and Sponaugle, 2009). These aspects can alter the survival of coral reefs in the face of climate change (e.g. following the deep and turbid reef refugia hypotheses; Bongaerts et al., 2010; Cacciapaglia and van Woesik, 2016; Glynn, 1996; van Woesik et al., 2012).

The generic coupled nature of the developed model offers many opportunities to improve modelling of coral-reef development by deriving specific modules for these factors. It is likely that such extensions are more fruitful than the computationally expensive, but ecologically rather irrelevant, diffusive boundary effects, which are at the basis of the thermal and flow micro-environments.

7.3. Essential data

This conceptual study was used to determine the key aspects in coral reef dynamics, both biological and physical. One such key aspect is the accurate prediction of significant events like bleaching and storms. Both result in substantial changes on the short-term, but also on the long-term as recovery of coral reefs is very slow. The developed model is able to give good insights into the damage due to bleaching events with relatively easily accessible data. However, data on storm damage is limited as well as data on the coral morphology and its development. Both the morphological aspects are key in predicting potential loss and decay of corals due to storm conditions.

Unfortunately, accurate data on the coral morphology and its development is hard to come by—largely due to the slow development, but also due to its dependency on short-term processes such as wave conditions. One approach to this issue is focusing on trait-based grouping of corals (Madin et al., 2016). Here, the coral morphology functions as one of the key traits (e.g. Zawada et al., 2019). This trait-based approach might also reduce the uncertainty of other essential parameters used in the model; e.g. the calcification constant (Madin et al., 2016).

8. Conclusions

The biophysical model developed in this study is a first attempt to couple the biology and physics of coral reefs to gain better insight into the complex world of coral reefs. The model design consists of a linear basis so new modules can easily be added. Furthermore, it is not site-specific and can be used worldwide with the correct tuning of parameters to region-specifies (e.g. the calcification constant).

The knowledge on the photosynthetic flow dependency is too scarce to justify the computational costs of implementation. This, however, does not implicate the decoupling of the biology from the physics due to the relevance of storm events on the development of coral reefs.

Improvements on the biophysical model might include the processes initiated by sedimentation and coral recruitment in a dynamical manner. These processes require detailed information on the hydrodynamics, and so a more intensive coupling between the biology and the physics would be necessary.

Author contributions

G.H., P.H., and J.D. designed the research; G.H. performed the research; G.H. analysed the data; G.H. coded the model; and G.H., P.H., J.D., C.S. and L.T. wrote the manuscript.

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Software availability

The software developed in this study is available on GitHub: https://github.com/ghendrickx/CoralModel. The biophysical model is open for collaboration. The model is written in Python 3. The model works independent from Delft3D Flexible Mesh—which is used for the hydrodynamic modelling in this study. However, the online coupling with Delft3D requires certain settings in Python.

Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.envsoft.2021.105103.

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